DEVONIAN MACROFLORAS

by WILLIAM G. CHALONER *and* ANNE SHEERIN

ABSTRACT. The appearance and extinction of plant genera has been the basis for various attempts (notably by Arber and by Kräusel) to develop a biostratigraphical subdivision of the Devonian Period based on plants. The seven plant assemblage zones recently proposed by Banks, covering the late Silurian to the close of the Devonian, represent a further refinement of earlier work. The ranges of seventy-one plant genera are plotted and related to these zones, and their occurrence in eight major geographical provinces is documented. The times of first appearance of some forty-two vegetative and reproductive characters are shown in diagrams which offer an alternative biostratigraphy based on innovation of structural features independent of the generic identity of the plants. The major features of Devonian vascular plant phylogeny are presented in terms of known generic ranges. The early Devonian macrofossil record is consistent with divergence of the lycopods, zosterophylls, trimerophytes, and progymnosperms from a single ancestral rhyniophyte stock between the Pridoli and mid-Devonian. Recent reports of a Ludlow age for part of the *Baragwanathia* flora, and of an *Archaeosigillaria* flora in late Silurian rocks in Libya present puzzling challenges to a plant-based biostratigraphy. The faunal basis for dating these Australian and African floras and their field relationships may require revision.

DESPITE the pioneering work of Hugh Miller (1859), Dawson (1862) and others in describing Devonian plant fossils in the latter half of the last century, it was not until Arber's review of 1921 that a serious attempt was made to assess the sequence of plants through the period in stratigraphical terms. Arber expounded the concept of 'two floras' within the Devonian—an early '*Psilophyton* flora' and a succeeding '*Archaeopteris* flora'. These two 'floras' had, in Arber's concept, both an evolutionary relationship (the former being more primitive than the latter) and a stratigraphical, sequential one. But he accepted that the two assemblages overlapped in some of their constituents. Although changing generic concepts and extended knowledge of their ranges have blurred much of Arber's picture, two basic items in his thinking have survived the passage of fifty years surprisingly well: first, that much of the major evolutionary diversification of land plants occurs within the Devonian Period; and secondly, that this offers a basis for subdividing Devonian time in terms of successive floras.

Kräusel (1937) developed Arber's ideas further in offering a three-fold division of the Devonian, with a *Hyenia* flora intercalated between Arber's two floras. Kräusel's approach was rather different from Arber's. He did not attempt to generate subdivisions within the Devonian on the basis of generic ranges, but rather enumerated the genera characteristic of the three classic subdivisions of the Lower, Middle, and Upper Old Red Sandstone. These three groups of genera he designated the *Psilophyton*, *Hyenia*, and *Archaeopteris* floras. Leclercq (1940) generally endorsed Kräusel's three-fold division, but suggested that *Protopteridium* (now *Rellimia*) was a more appropriate characteristic genus of the middle unit. Since that time many authors have attempted reviews of plant ranges within the Devonian—e.g. Seward (1933) on a world-wide basis; Read and Mamay (1964) for the USA; Banks (1966) for New York State; Andreeva *et al.* (1962) for Russia; Ananiev (1959) for Siberia; and Lee and Tsai (1978*c*) for China. There have also been a number of important reviews of the geographical distribution of Devonian plants (Petrosian 1968; Vakhrameev *et al.* 1970; Edwards 1973; Banks 1975*c*). Some authors (Banks, Edwards) have emphasized the general lack of a conspicuous regional character in Devonian floras (at least compared with the subsequent Carbo-Permian differentiation); while others (e.g. Petrosian) have emphasized the existence of many regional 'endemic' genera (e.g. in Siberia and Kazakhstan) which are suggestive either of climatic differences or more probably some barrier restricting migration, with resulting biological isolation. The series of seven plant assemblage zones within the late Silurian-Devonian interval, proposed by Banks (1979), represents a major contribution to the use of plants in Devonian

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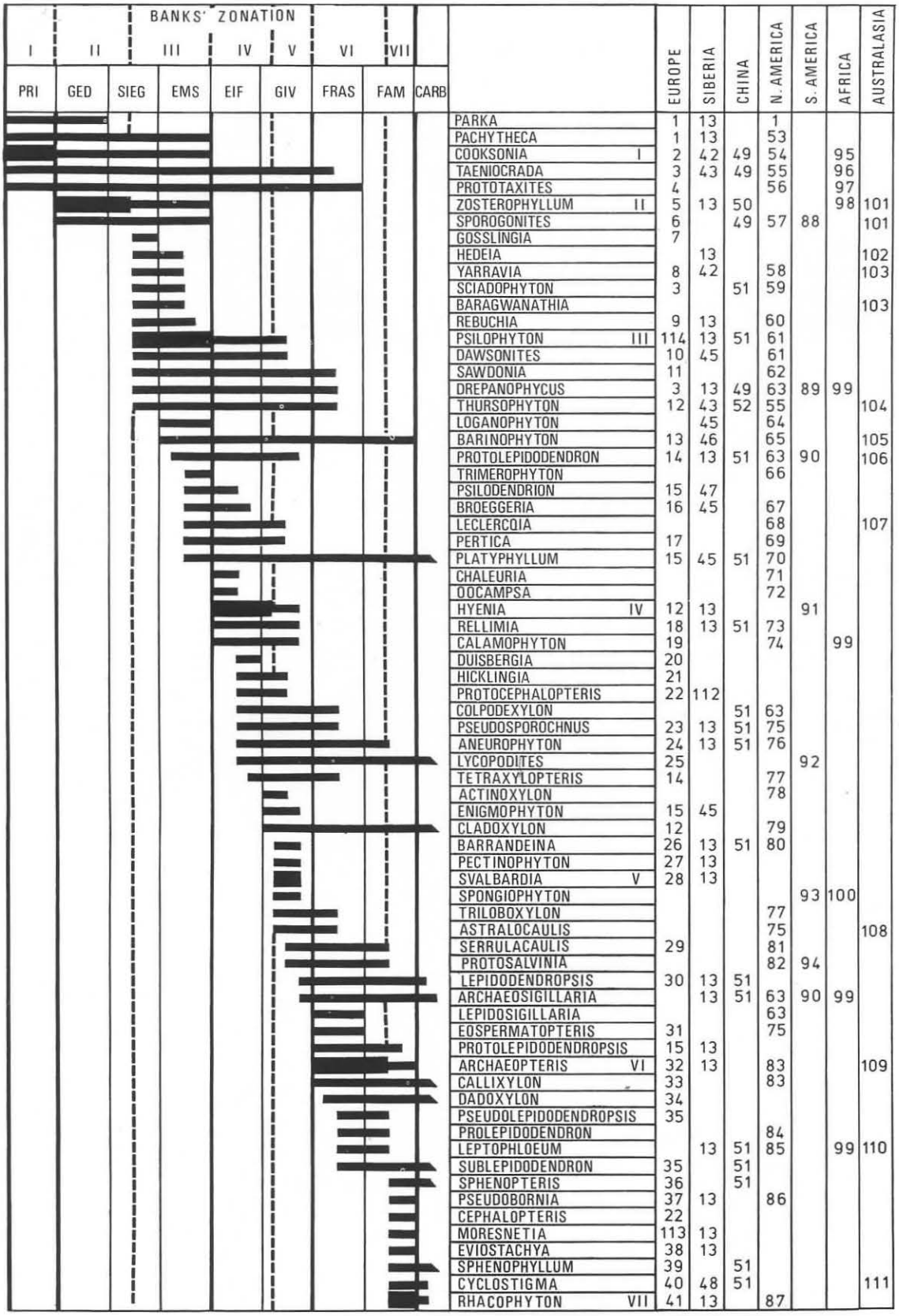
biostratigraphy (text-fig. 1). Before examining these zones, it is worth considering two general problems arising when using plants rather than animal fossils as a basis for biostratigraphy. First, land plants typically occur in continental deposits, and in those restricted environments which favour their preservation. Many of the most productive fossil plant occurrences have been 'lenses' of limited horizontal and vertical extent, seen only in a single exposure. As a result their location even within regional lithostratigraphical units may be obscure, and their precise correlation with a faunally dated marine sequence virtually impossible. Palynology offers perhaps the single most important means of relating isolated plant-bearing sections to at least the more widely recognized stages of the Devonian. The palynological dating of the Rhynie Chert (see Westoll *in* House *et al.* 1977) and the Trout Valley flora in Maine (Andrews *et al.* 1977) are cases in point.

The second general problem in dealing with plant fossils is that the majority of Devonian plants are known only in a fragmentary state, and in most cases genera are based on single, detached plant organs (leaves, axes, sporangia, seeds). This fragmentation, aggravated by different preservation-states of parts of the same plant, means that the same plant species may appear in the fossil state in several different forms. For example, the relationship of the widespread late Devonian genus *Callixylon*, based on permineralized wood, and the genus *Archaeopteris*, based on compression of leafy shoots, went unsuspected for many years until Beck (1960) found them in organic connection. An analogous problem concerns the relationship between the genera *Protopteridium*, *Rellimia*, *Aneurophyton*, *Ptilophyton*, and *Eospermatopteris*, which some authors (Remy and Remy 1977) have regarded as synonyms. The true relationship of these genera has been obscured by problems of nomenclature and of preservation state, and is still not resolved (Bonamo 1977). These and other difficulties peculiar to the development of a plant-based zonation, are considered more fully by Banks (1979).

TEXT-FIG. 1. Stratigraphical ranges of some genera of Devonian plant macrofossils, and their geographical distribution. The numbered zones (top left) are those of Banks 1979, the appropriate number being shown after the characteristic genus of each zone in the generic list. The range of each zonal genus is shown with a line of double thickness within its own zone. References given below are generally the most recent contribution, which will lead to earlier sources, rather than the first record or the most complete. Where a genus occurs in a given region in the Carboniferous, but not the Devonian, no record is shown (e.g. *Archaeosigillaria* in Europe).

1 = Niklas 1976; 2 = Edwards 1970*a*; 3 = Kräusel and Weyland 1930; 4 = Kräusel and Weyland 1934; 5 = Edwards 1975; 6 = Andrews 1960; 7 = Edwards 1970*b*; 8 = Danzé-Corsin 1956; 9 = Mägdefrau 1938; 10 = Chaloner 1972; 11 = Zdebska 1972; 12 = Kräusel and Weyland 1926; 13 = Petrosian 1968; 14 = Mustafa 1975; 15 = Høeg 1942; 16 = Nathorst 1915; 17 = Høeg 1973; 18 = Leclercq and Bonamo 1971; 19 = Leclercq and Andrews 1960; 20 = Kräusel and Weyland 1929; 21 = Edwards 1976; 22 = Schweitzer 1968; 23 = Leclercq and Banks 1962; 24 = Leclercq 1940; 25 = Kräusel and Weyland 1937; 26 = Obrhel 1961; 27 = Høeg 1935; 28 = Kräusel and Weyland 1960; 29 = Stockmans 1968; 30 = Kiltorcan, Ireland (unpublished); 31 = Kräusel and Weyland 1935*a*; 32 = Johnson 1911; 33 = Zalessky 1911; 34 = Rilett and Taylor 1952; 35 = Schweitzer 1969; 36 = Baily 1861; 37 = Nathorst 1894; 38 = Leclercq 1957; 39 = Nathorst 1902; 40 = Chaloner 1968; 41 = Leclercq 1951; 42 = Høeg 1967; 43 = Ananiev and Krasnov 1962; 45 = Ananiev 1959; 46 = Lepekhina *et al.* 1962; 47 = Lepekhina 1960; 48 = Ananiev and Eganov 1957; 49 = Lee and Tsai 1978*a*; 50 = Lee and Tsai 1978*b*; 51 = Lee and Tsai 1978*c*; 52 = Anon. 1974; 53 = McGregor and Terasmae 1959; 54 = Banks 1972; 55 = Andrews *et al.* 1977; 56 = Arnold 1952; 57 = Dorf and Rankin 1962; 58 = Canwright 1970; 59 = Steinmann 1929; 60 = Hueber 1972; 61 = Kasper *et al.* 1974; 62 = Gensel *et al.* 1975; 63 = Grierson and Banks 1963; 64 = Kräusel and Weyland 1961; 65 = Arnold 1935; 66 = Hopping 1956; 67 = Dorf 1934; 68 = Banks *et al.* 1972; 69 = Kasper and Andrews 1972; 70 = Arnold 1936; 71 = Andrews *et al.* 1974; 72 = Andrews *et al.* 1975; 73 = Bonamo 1977; 74 = Bonamo and Banks 1966; 75 = Banks 1966; 76 = Serlin 1977; 77 = Scheckler and Banks 1971; 78 = Matten 1968; 79 = Matten 1974; 80 = Schopf 1964; 81 = Hueber 1961; 82 = Niklas and Phillips 1976; 83 = Beck 1964; 84 = Arnold 1939; 85 = Dawson 1862; 86 = Mamay 1962; 87 = Cornet *et al.* 1976; 88 = Frenguelli 1951; 89 = Menendez 1965; 90 = Kräusel and Dolianiti 1957; 91 = Frenguelli 1954; 92 = Dolianiti 1967; 93 = Kräusel 1960; 94 = Niklas *et al.* 1976; 95 = Daber 1971; 96 = Lemoigne 1967; 97 = Koeniguer 1975; 98 = Plumstead 1977; 99 = Plumstead 1967; 100 = Chaloner *et al.* 1974; 101 = Lang and Cookson 1930; 102 = Cookson 1935; 103 = Lang and Cookson 1935; 104 = Lang and Cookson 1927; 105 = Dun 1898; 106 = Walkom 1928; 107 = Fairon-Demaret 1974; 108 = Harris 1929; 109 = McCoy 1876; 110 = McCoy 1874; 111 = Feistmantel 1890; 112 = Ananiev 1960; 113 = Stockmans 1948; 114 = Banks *et al.* 1975.



		EUROPE	SIBERIA	CHINA	N. AMERICA	S. AMERICA	AFRICA	AUSTRALASIA
PARKA		1	13		1			
PACHYTHECA		1	13		53			
COOKSONIA	I	2	42	49	54		95	
TAENIOCRADA		3	43	49	55		96	
PROTOTAXITES		4			56		97	
ZOSTEROPHYLLUM	II	5	13	50			98	101
SPOROGONITES		6		49	57	88		101
GOSSLINGIA		7						
HEDEIA			13					102
YARRAVIA		8	42		58			103
SCIADOPHYTON		3		51	59			
BARAGWANATHIA								103
REBUCHIA		9	13		60			
PSILOPHYTON	III	114	13	51	61			
DAWSONITES		10	45		61			
SAWDONIA		11			62			
DREPANOPHYCUS		3	13	49	63	89	99	
THURSOPHYTON		12	43	52	55			104
LOGANOPHYTON			45		64			
BARINOPHYTON		13	46		65			105
PROTOLEPIDODENDRON		14	13	51	63	90		106
TRIMEROPHYTON					66			
PSILODENDRION		15	47					
BROEGGERIA		16	45		67			
LECLERCQIA					68			107
PERTICA		17			69			
PLATYPHYLLUM		15	45	51	70			
CHALEURIA					71			
OOCAMPSA					72			
HYENIA	IV	12	13			91		
RELLIMIA		18	13	51	73			
CALAMOPHYTON		19			74		99	
DUISBERGIA		20						
HICKLINGIA		21						
PROTOCEPHALOPTERIS		22	112					
COLPODEXYLON				51	63			
PSEUDOSPOROCHNUS		23	13	51	75			
ANEUROPHYTON		24	13	51	76			
LYCOPODITES		25				92		
TETRAXYLOPTERIS		14			77			
ACTINOXYLON					78			
ENIGMOPHYTON		15	45					
CLADOXYLON		12			79			
BARRANDEINA		26	13	51	80			
PECTINOPHYTON		27	13					
SVALBARDIA	V	28	13					
SPONGIOPHYTON						93	100	
TRILOBOXYLON					77			
ASTRALOCAULIS					75			108
SERRULACAULIS		29			81			
PROTOSALVINIA					82	94		
LEPIDODENDROPSIS		30	13	51				
ARCHAEOSIGILLARIA			13	51	63	90	99	
LEPIDOSIGILLARIA					63			
EOSPERMATOPTERIS		31			75			
PROTOLEPIDODENDROPSIS		15	13					
ARCHAEOPTERIS	VI	32	13		83			109
CALLIXYLON		33			83			
DADOXYLON		34						
PSEUDOLEPIDODENDROPSIS		35						
PROLEPIDODENDRON					84			
LEPTOPHLOEUM			13	51	85		99	110
SUBLEPIDODENDRON		35		51				
SPHENOPTERIS		36		51				
PSEUDOBORNIA		37	13		86			
CEPHALOPTERIS		22						
MORESNETIA		113	13					
EVIOSTACHYA		38	13					
SPHENOPHYLLUM		39		51				
CYCLOSTIGMA		40	48	51				111
RHACOPHYTON	VII	41	13		87			

GENERIC RANGES AND BANKS' ZONES

Text-fig. 1 sets out the known ranges of a number of plant genera in terms of the classical stages of the late Silurian and Devonian, and enumerates their occurrence in different regions. The precision which can be claimed for their range records is limited by the factors reviewed above. We have chosen to present genera which seem to be reasonably well-defined, and which (with a few exceptions) occur in more than one depositional basin, so contributing to the possibility of inter-regional correlation. We have also included a few genera (e.g. *Parka*, *Spongiophyton*, *Protosalvinia*) which, although not vascular plants, either share some vascular plant characteristics (e.g. a cuticle or resistant spores) or commonly occur in association with vascular plants. In these aspects, and for some details of ranges, text-fig. 1 differs from the table given by Banks (1979).

Banks' plant assemblage zones are essentially based on such data; each of his seven zones is designated by a Roman numeral and a characteristic genus. These zones are shown at the top of text-fig. 1. In each case the time range of the characteristic genus is shown with a broader width of bar within its zone; and the zone number is shown opposite the relevant genus in the centre column.

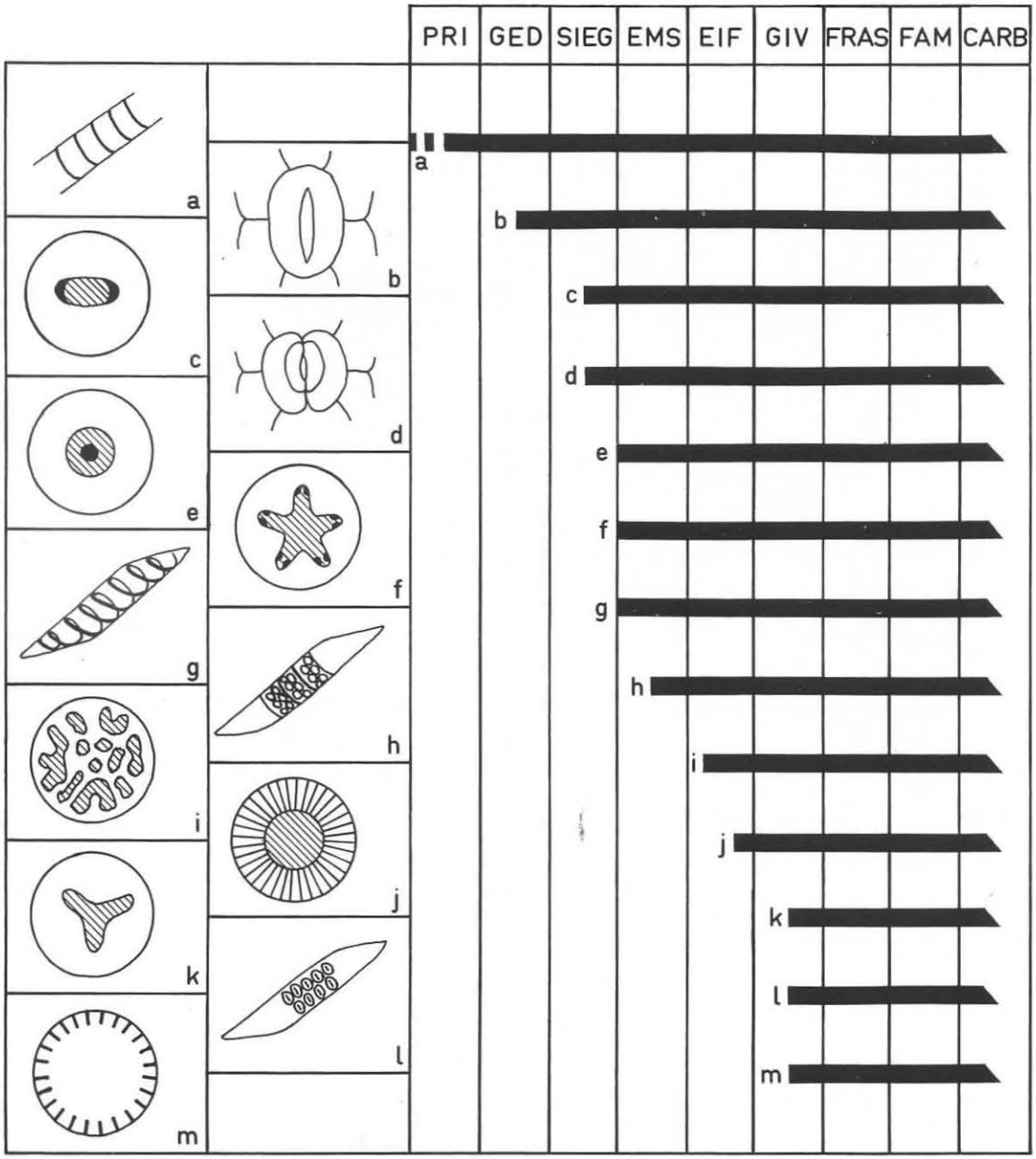
For example, his zone I of approximately Přídoli or Downton age is the *Cooksonia* Zone. It can be seen that the range of each characteristic genus (with the exception of *Svalbardia*) exceeds its designated zone, and although Banks indicates additional characteristic genera for each assemblage there is inevitably a subjective element in the delimitation of the zones. While he enumerates the locations of typical representatives of each of the assemblages, Banks does not specify a type section for each zone, and indeed it may be desirable to postpone this until the consistency and general applicability of his zones is assessed. Their time relationship with palynological zones (considered more fully by Banks 1979) will be particularly important in this respect, as more palynological data are accrued.

EVOLUTIONARY INNOVATION AND BIOSTRATIGRAPHY

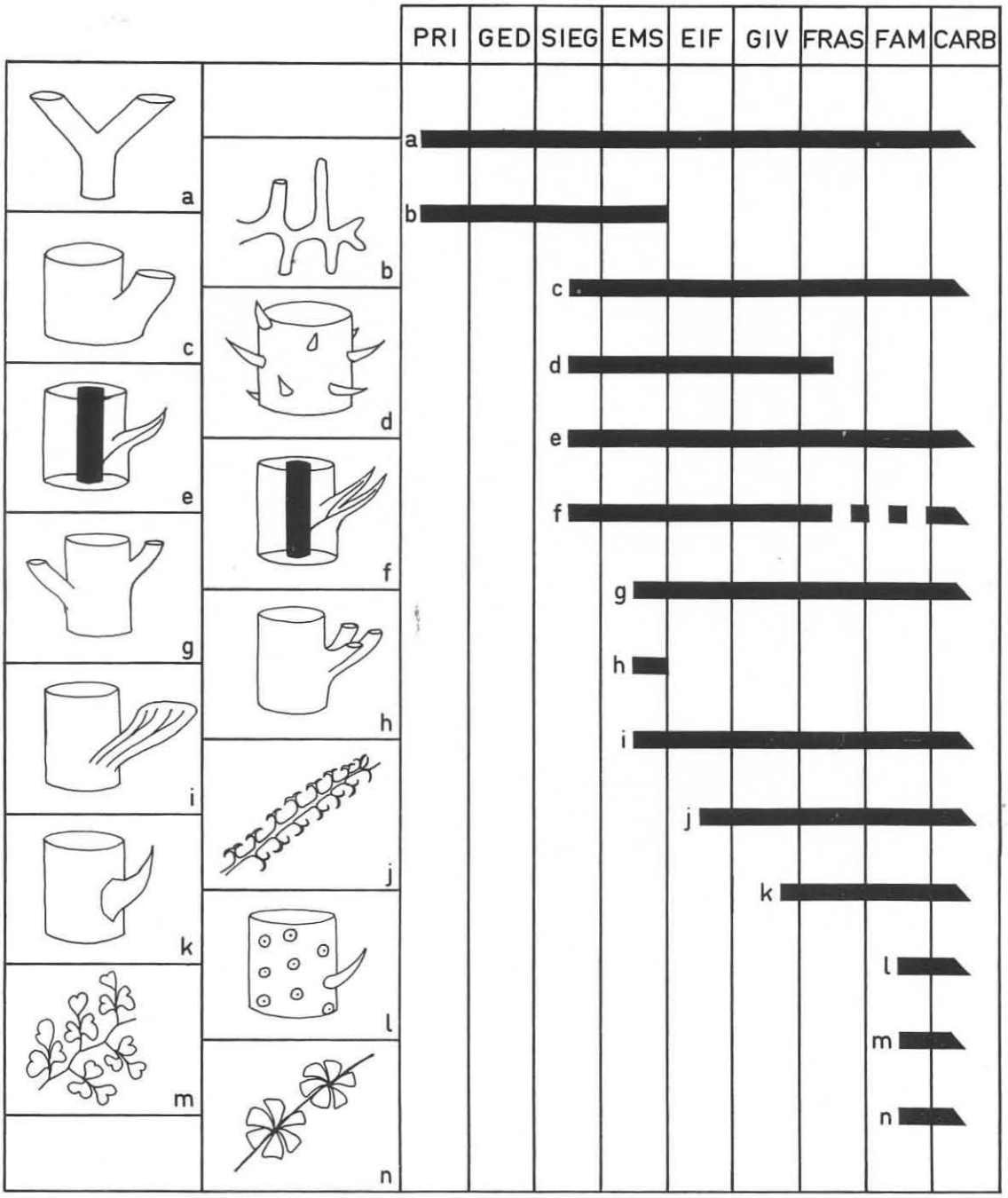
Many of the major 'innovations' in plant structures and reproductive biology occurred within the Devonian or latest Silurian. Some of these events are summarized in the bar diagrams of text-figs. 2–4. Many of these constitute 'first occurrences' of very basic attributes, which became widespread in diverse groups later in geological time (e.g. tracheids, stomata, secondary thickening of the stele, etc.; text-figs. 2*a*, *b*, *j*) while others are limited to one genus, and are of relatively short duration (e.g. the branched sporophyll of *Leclercqia*, text-fig. 4*h*). Other reproductive features, such as the fusiform sporangium with longitudinal dehiscence, first appear in one genus (*Dawsonites*, text-fig. 4*d*), but the same type of sporangium is then sustained in a series of genera of trimerophytes and progymnosperms, which were probably derived from *Dawsonites*-like ancestors through the remainder of the Devonian. Other features such as the attainment of heterospory (text-fig. 4*k*) and the seed (text-fig. 4*o*) evidently arose polyphyletically, but none the less constitute a widely recognizable event in their 'first occurrence' (Pettitt and Beck 1968; Chaloner *et al.* 1977). Banks (1979) has emphasized that such levels of evolutionary attainment can usefully supplement the assignment of a flora to one of his zones, without involving generic identification. To illustrate this concept text-figs. 2–4 are drawn up in a purely 'structural' form, without relation to particular generic ranges.

EVOLUTION OF PLANT SIZE

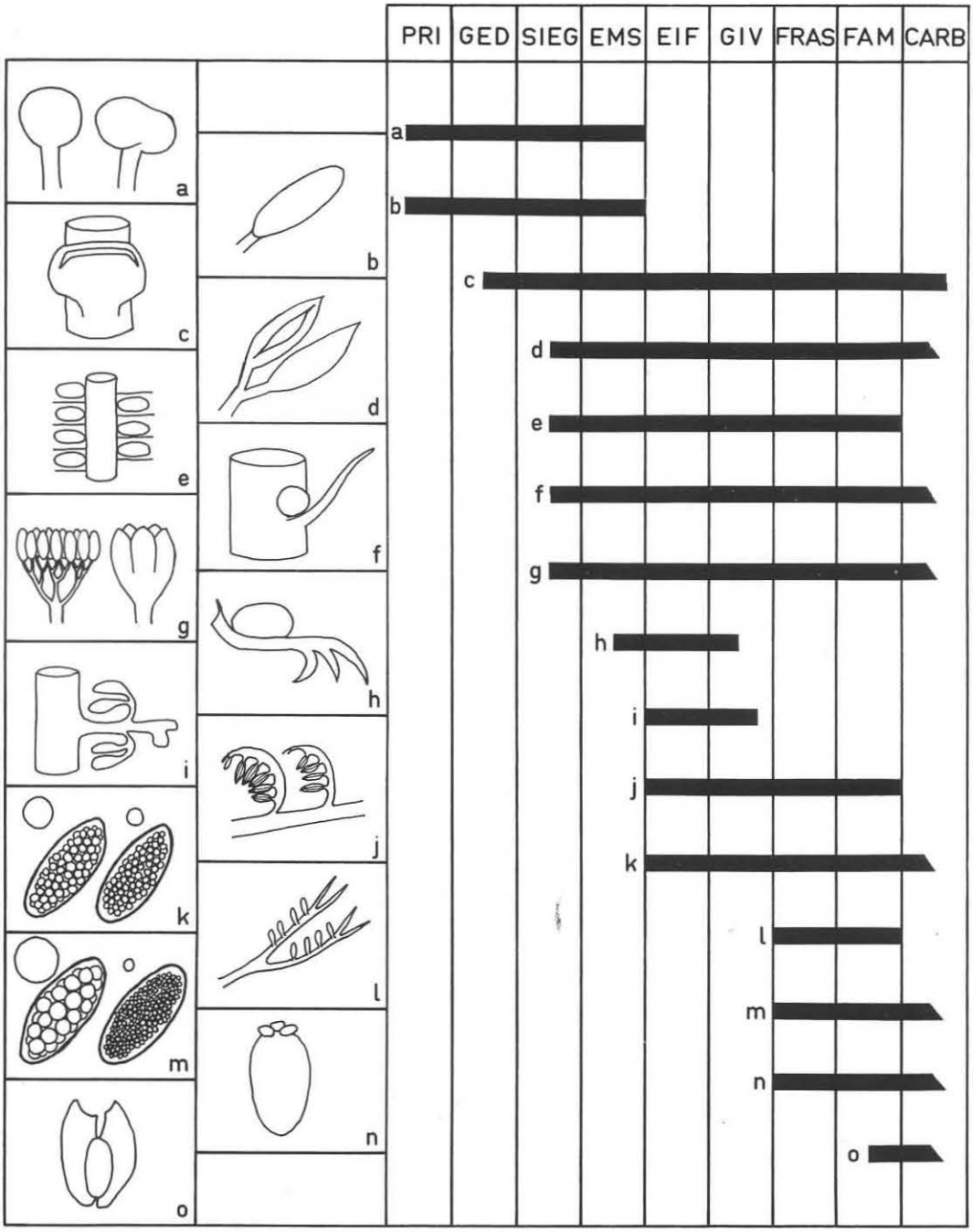
One aspect of plant evolution in the Devonian is of broad biological significance; namely the maximum potential height of individual plants. It is evident in general terms that following *Cooksonia* in the late Silurian, only a few centimetres in height, progressively larger plants evolved until by the end of the Devonian *Archaeopteris* (with *Callixylon* wood) was more than a metre in diameter, and presumably formed large forest trees. Zimmermann (1930) plots a generalized graph to indicate this height increase in plants through the Devonian, relating his data to a small number of named genera. Direct evidence of plant height is obviously only rarely available from fossil material;



TEXT-FIG. 2. Diagrammatic record of the time of first appearance of various anatomical features of Devonian fossil plants: (*a*) tracheids with annular thickenings (e.g. in axes of Lang 1937; see also Edwards and Davies 1976); (*b*) stoma with apparently interconnected guard cells (e.g. in *Zosterophyllum*, Lele and Walton 1961); (*c*) stele with xylem of elliptical cross-section with exarch protoxylem (e.g. in *Gosslingia*, Edwards 1970*b*); (*d*) stoma with paracytic subsidiary cells (e.g. in *Drepanophycus*, Stubblefield and Banks 1978); (*e*) stele with xylem cylindrical and endarch (e.g. in *Rhynia*, Kidston and Lang 1917); (*f*) stele with xylem of stellate cross-section (e.g. in *Asteroxylon*, Kidston and Lang 1920); (*g*) tracheids with spiral thickenings (e.g. in *Asteroxylon*, Kidston and Lang 1920); (*h*) tracheids with mesh-like wall, simulating pits, between scalariform bars (e.g. in *Psilophyton*, Banks *et al.* 1975); (*i*) polystele (e.g. in *Calamophyton*, Schweitzer 1973); (*j*) secondary xylem (e.g. in *Rellimia*, Mustafa 1975); (*k*) trilobed stele related to branch arrangement (e.g. in *Triloboxylon*, Matten 1974); (*l*) tracheids with bordered pits (e.g. in *Leclercqia*, Grierson 1976); (*m*) secondary cortex or periderm (e.g. in *Triloboxylon*, Scheckler and Banks 1974).



TEXT-FIG. 3. Diagrammatic record of the time of first appearance of various features of the vegetative morphology of Devonian fossil plants: (*a*) equal dichotomy (e.g. in *Cooksonia*, Obrhel 1962); (*b*) H-branching (e.g. in *Zosterophyllum*, Høeg 1942); (*c*) overtopping: ratio of main axis diameter to that of overtopped lateral 2:1 (e.g. in '*Psilophyton princeps*', Strathmore Group, of Lang 1932, but see also earlier records of the genus *Psilophyton*, e.g. Banks 1979, where age and/or branch status is less secure); (*d*) enations (e.g. in *Sawdonia*, Hueber 1971); (*e*) vascularized microphylls (e.g. in *Drepanophycus*, Kräusel and Weyland 1935*b*); (*f*) forked microphylls (e.g. in *Sugambrophyton*, Schmidt 1954); (*g*) overtopping: ratio of main axis to overtopped lateral *c*. 4:1 (e.g. in *Pertica*, Kasper and Andrews 1972); (*h*) 'trichotomy' of overtopped laterals (e.g. in *Trimerophyton*, Hopping 1956); (*i*) vascularized wedge-shaped megaphylls (e.g. in *Platyphyllum*, Høeg 1942); (*j*) planated, ?pinnate megaphyll (e.g. in *Aneurophyton*, Leclercq 1940); (*k*) expanded leaf base, i.e. leaf cushion or leaf cushion precursor? (e.g. in *Archaeosigillaria*, Grierson and Banks 1963); (*l*) leaf abscission (e.g. in *Cyclostigma*, Chaloner 1968); (*m*) sphenopterid megaphylls (e.g. in *Sphenopteris*, Baily 1861); (*n*) whorled leaves (e.g. in *Sphenophyllum*, Nathorst 1902).



TEXT-FIG. 4. Diagrammatic record of the time of first appearance of various types of reproductive structure in Devonian fossil plants: (*a*) terminal rounded sporangia (e.g. in *Cooksonia*, Obrhel 1962); (*b*) terminal ellipsoid sporangia (e.g. in *Eorhynia*, Ishchenko 1975); (*c*) lateral reniform sporangia with transverse dehiscence (e.g. in *Zosterophyllum*, Edwards 1975); (*d*) terminal fusiform sporangia with longitudinal dehiscence (e.g. in *Dawsonites*, Croft and Lang 1942); (*e*) small lateral sporangia associated with appendages in biseriate arrangement (e.g. in *Krithodeophyton*, Edwards 1968); (*f*) sporangia in axils of microphyllous leaves (e.g. in *Baragwanathia*, Lang and Cookson 1935); (*g*) corymbose aggregation of fusiform sporangia (*Hedeia*) and synangial aggregation of sporangia (*Yarravia*) (Cookson 1935; Lang and Cookson 1935); (*h*) sporangia borne singly on adaxial surface of sporophylls (e.g. in *Leclercqia*, Banks *et al.* 1972); (*i*) sporangia borne on recurved bifurcating side-branches of a dichotomous sporangiophore (e.g. in *Calamophyton*, Leclercq and Andrews 1960); (*j*) fusiform sporangia borne in clusters on pinnate fertile organs (*Rellimia*, Leclercq and Bonamo 1971); (*k*) sporangia with morphologically distinct spores of two sizes (e.g. in *Chaleuria*, Andrews *et al.* 1974); (*l*) sporangia on megaphylls (e.g. in *Archaeopteris*, Phillips *et al.* 1972); (*m*) sporangia with mega- and microspores (e.g. in *Archaeopteris*, Pettitt 1965); (*n*) megaspore tetrad: one large, presumed fertile, three small, presumed abortive (e.g. in *Cystosporites*, Chaloner and Pettitt 1964); (*o*) radiospermic (*Archaeosperma*) and platyspermic (*Spermolithus*) seeds (Pettitt and Beck 1968; Chaloner *et al.* 1977).

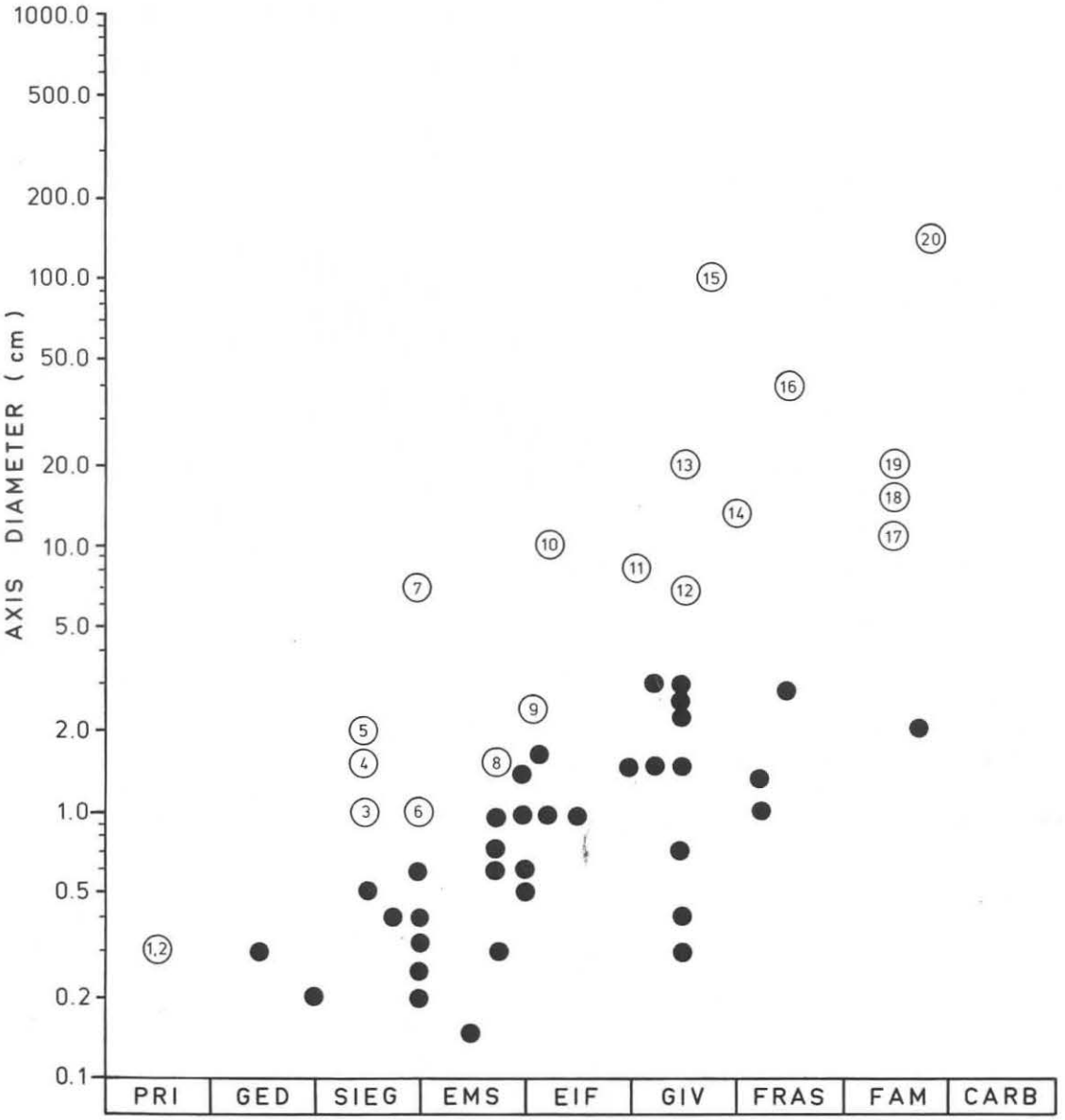
even when considerable lengths of stems are preserved, usually lying parallel to the bedding planes, only a mimimum height of the living plant is represented. Obviously, stem diameter is a measurement more readily made on many specimens; in very broad terms, diameter correlates with height, in that height cannot be achieved without a corresponding increase in rigidity and girth. The selective pressure to gain height, and so greater access to light in competition with adjoining plants, would seem to be a very basic feature of plant biology. Height would also potentially give access to wind for the dispersal of propagules to sites of further colonization. Devonian plants increased their girth by means of a number of different strategies. Some adopted prolonged primary growth; others, secondary growth, principally of the xylem (e.g. in progymnosperms); still others developed secondary growth of the cortex, with or without secondary growth of the xylem (e.g. *Triloboxylon*, and presumably the large arborescent lycopods such as *Cyclostigma*). The evidence available suggests that these various ways of developing large stems were evolved independently in different groups, which were inevitably competing with one another.

The maximum observed diameter from a wide range of Devonian vascular plants, plotted on a log scale (text-fig. 5), seems to bear out this general, approximately logarithmic, increase through the Devonian Period. This one simple parameter also represents the increasing potential of plants to form more complex plant communities, in which ecological 'stratification' of the constituents would evolve, with different micro-environments at different levels of light intensity and humidity; these would, in turn, represent an increasing range of habitats for animal colonization. An assortment of plant axes at any horizon will include pieces of major upright stems, their branches (of all sizes), and of course the stems of much smaller plants. In most cases we have little evidence as to the status of a given fossil axis within the whole plant. For this reason we attach significance to the gradient of the upper 'surface' of the totality of axial diameters plotted, and hence give source citations only for the larger axes in each time interval (numbered circles in text-fig. 5).

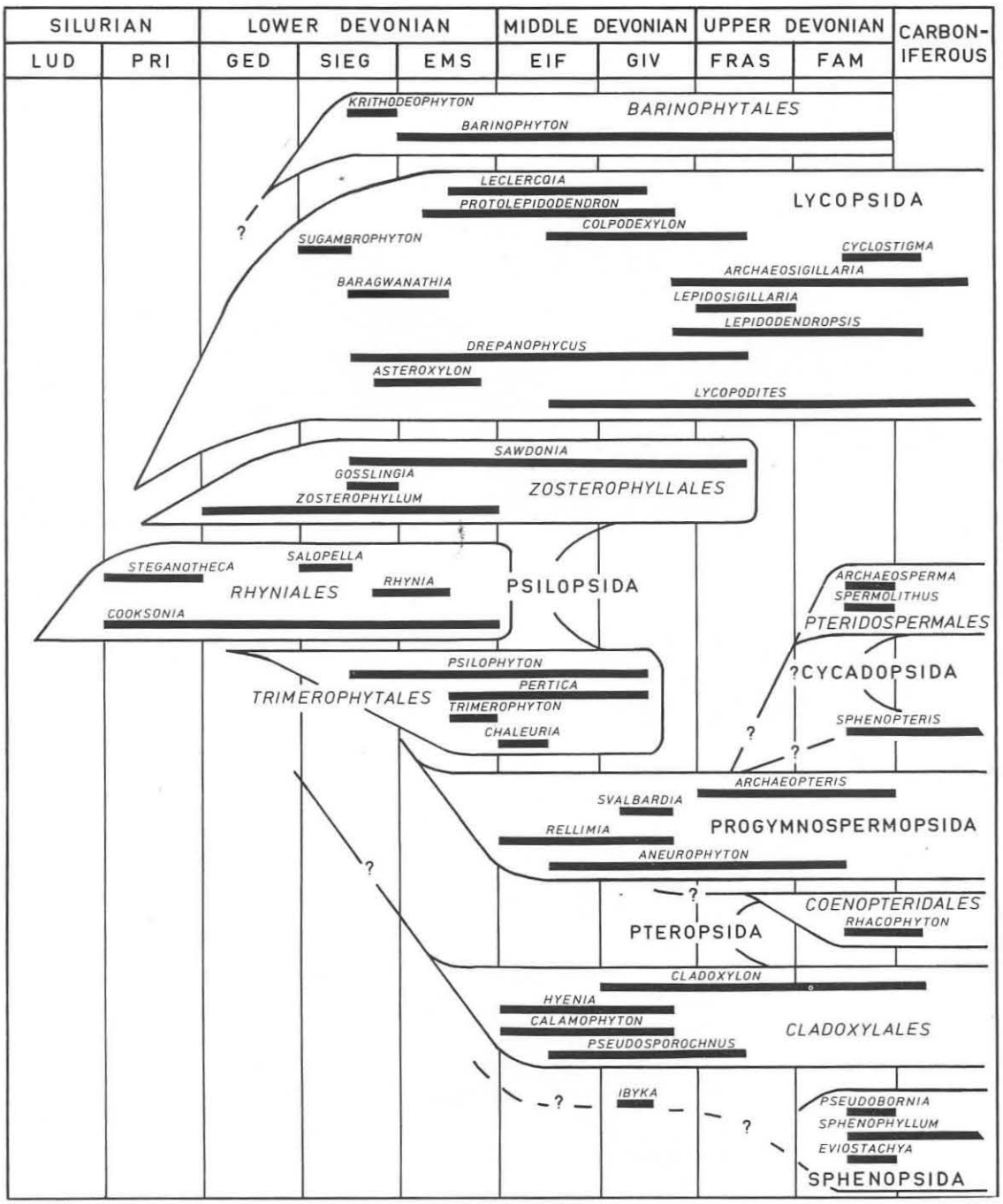
It is interesting to speculate on the changes in reproductive strategy which would be favoured by increasingly complex plant communities, of greater productivity and casting deeper shade. Broadly speaking, modern trees of closed forests produce seeds with a considerable food reserve and limited mobility, while those of pioneer tree species (e.g. birch and poplar, of temperate latitudes) have much more limited food reserves, so that they are smaller and more easily wind-dispersed. The food reserve carried by a propagule governs its ability to grow even in dense shade to a height at which it can reach a light intensity sufficient to sustain photosynthesis for its independent growth. The evolution from homospory through heterospory to the seed may in some cases have been closely linked biologically with the increasing size of the parent plants, and the corresponding increase in complexity of plant communities. The prevalence of homospory in early Devonian plants may also be related to the apparently world-wide extent of many of the early land plants (Banks 1975*c*); homosporous plants (pteridophytes and bryophytes) with their minute spores, each having the potential of producing in isolation a new sporophyte plant, have a unique potential for long-distance transport. This is illustrated by their being the predominant early colonizers of isolated, newly available land habitats (e.g. Krakatoa; Ridley 1930). Increased propagule size (heterospory, and the seed habit) although favouring survival in closed plant communities, would have diminished the potential for long-distance (inter-continental) dispersal. This reduced mobility may have had an important role in the development of regional floras in late Devonian and Carboniferous times.

PHYLOGENY AND STRATIGRAPHY

Evidence both from fossils and comparative study of living plants seems to favour a monophyletic origin of vascular plants. The common biochemical attributes of the composition of cell walls, type of food reserves, chlorophyll pigments, and such basic shared anatomical features as archegonia, stomata, and tracheidal elements suggests a common origin for tracheophytes on these grounds alone. The late Silurian-Devonian macrofossil record, presented in diagrammatic form in text-fig. 6, in terms of selected genera, is consistent with this. In the last decade there has been much debate as to how far microfossil evidence favours the existence of pre-Přídoli vascular plants (Banks



TEXT-FIG. 5. Maximum observed axis diameter for late Silurian and Devonian vascular plants plotted on a log scale. The stages of the Devonian Period, in abbreviated form, and their junction with the Carboniferous are shown as the horizontal axis. There appears to be a general increase in maximum axis diameter through the Devonian Period. Each marked spot represents a published axis diameter, but only the higher values (numbers in the figure) for each stage are keyed with references as follows: 1 = *Cooksonia* (Banks 1969); 2 = *Taeniocrada* (Obrhel 1962); 3 = *Thursophyton* (Kräusel and Weyland 1930); 4 = *Taeniocrada* (Kräusel and Weyland 1930); 5 = *Drepanophycus* (Kräusel and Weyland 1930); 6 = *Asteroxylon* (Kidston and Lang 1920); 7 = *Baragwanathia* (Lang and Cookson 1935); 8 = *Pertica* (Andrews *et al.* 1977); 9 = *Arctophyton* (Schweitzer 1968); 10 = *Calamophyton* (Schweitzer 1973); 11 = *Pseudosporochnus* (Leclercq and Banks 1962); 12 = *Amphidoxodendron* (Grierson and Banks 1963); 13 = *Pseudosporochnus* (Potonié and Bernard 1904); 14 = *Protolepidodendropsis* (Høeg 1942); 15 = *Eospermatopteris* (Goldring 1924); 16 = *Lepidosigillaria* (White 1907); 17 = *Sublepidodendron* (Schweitzer 1969); 18 = *Pseudolepidodendropsis* (Schweitzer 1969); 19 = *Cyclostigma* (Schweitzer 1969); 20 = *Callixylon* (Arnold 1934).



TEXT-FIG. 6. A phylogeny of late Silurian and Devonian vascular plants. Ranges of representative genera are shown as solid bars, enclosed within outlines representing higher taxa. Within the Lycopsida, genera believed to be of close affinity are in vertical proximity to one another, but ordinal groupings are not attempted.

1975*a*, *b*; Chaloner 1970, 1975; Edwards and Davies 1976; Gray and Boucot 1977; Pratt *et al.* 1978). While triradiate spores and fragments of resistant, cuticle-like membranes showing outlines of cells undoubtedly extend back to the early Silurian, and tracheid-like cells possibly to the Ludlow, we still have no evidence of any two of these attributes occurring together in a single species of organism before the Přídoli.

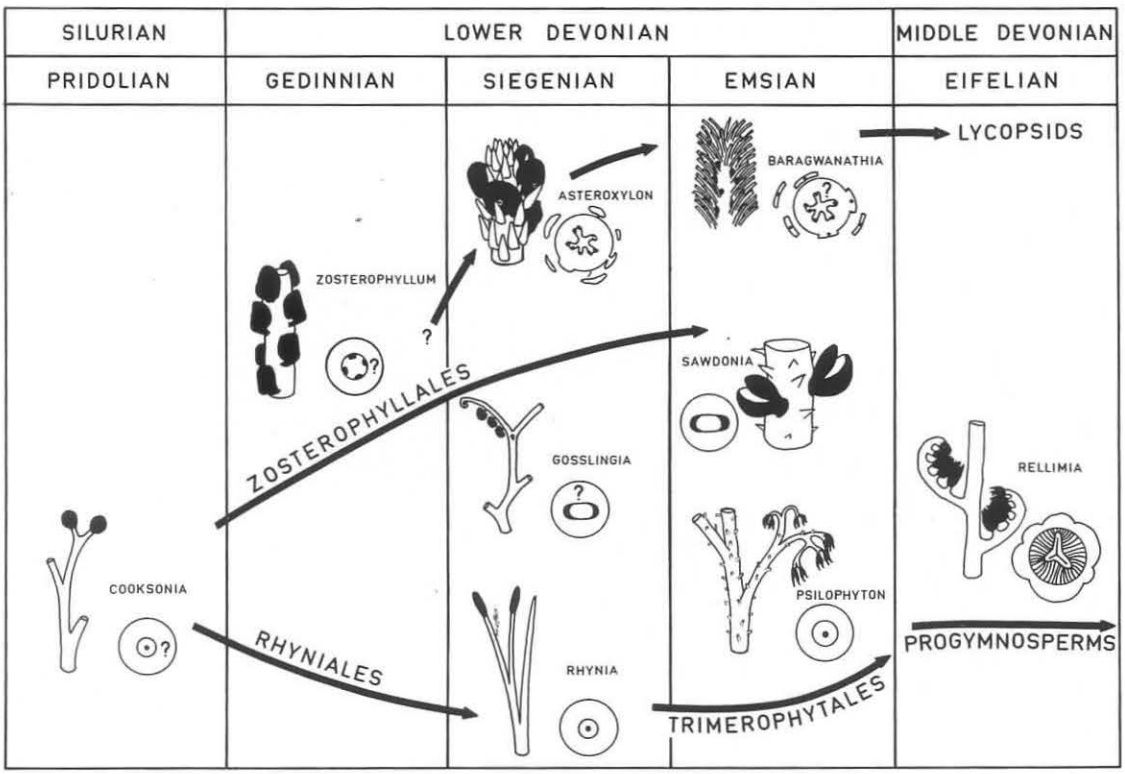
The basic features of the evolutionary relationships suggested in text-fig. 6 have been amply explored elsewhere (Banks 1968, 1975*a*; Beck 1970; Bonamo 1975). The only purpose of this diagram is to link the main lines of divergence of suprageneric groups to the ranges of typical genera on a time scale. We have chosen to recognize the Tracheophyta (i.e. all the plants in the diagram) as a single Division, subdivided into the classes Psilopsida, Lycopsida, Sphenopsida, Pteropsida, Progymnospermopsida, and Cycadopsida; orders are shown within these classes where appropriate. This follows the treatment of Sporne (1975) rather than that of most American authors (e.g. Banks 1968; Foster and Gifford 1974; Bierhorst 1974) who generally give different taxonomic status (rank) to the groups here treated as the orders Rhyniales, Zosterophyllales, and Trimerophytales.

Two aspects of text-fig. 6 justify brief mention. The Devonian record of the ferns has been considerably 'eroded' in the last twenty years, with the recognition of the progymnosperms. Various genera (*Archaeopteris*, *Rellimia*, *Aneurophyton*) seen by earlier workers as having fern-like attributes (e.g. compound leaves, bearing sporangia; seemingly circinate vernation; similarity of leaf trace anatomy to that of Carboniferous Coenopteridales, etc.) have been shown to have equally significant resemblances to the progymnosperms (Andrews 1970; Beck 1970; Bonamo 1975)—particularly in their possession of gymnosperm-like xylem elements and secondary thickening. This has extended the line of plausible precursors of the seed ferns (Pteridospermales) and other gymnosperms back through the Devonian progymnosperms and Trimerophytales to the Rhyniales (text-fig. 6), and leaves only a relatively small group of broadly cladoxylalean plants, and a few late Devonian genera with clepsydroid leaf traces, as precursors of the Carboniferous pteropsids.

The Sphenopsida (which include the living *Equisetum* and Carboniferous *Calamites*) also have a less secure Devonian record now than that accepted a few years ago. The demonstration by Leclercq and Schweitzer (1965) that *Calamophyton* is not an articulate but a cladoxylalean (pteropsid) plant, weakened the claim of the related *Hyenia* and *Protohyenia* to affinity with the sphenopsids. The pre-Upper Devonian record of the Sphenopsida is still in an uncertain state, in spite of subsequent discoveries of the early Devonian putative sphenopsid done *Equisetophyton* (Schweitzer 1972), the Middle Devonian stem *Honseleria* (Mustafa *in* Remy and Remy 1977), which apparently possessed whorled leaves and a pith cavity, and fertile shoots of the Givetian genus *Ibyka* (Skog and Banks 1973). The earliest widely accepted reports of Devonian sphenopsids remain the Famennian records of *Pseudobornia*, *Eviostachya*, and *Sphenophyllum*, which constitute unambiguous evidence of the group.

CONFLICTS BETWEEN FLORAL AND FAUNAL EVIDENCE

There are currently two instances where there is evident conflict between the Devonian plant sequence outlined here, and faunal evidence of the age of the floras. The first of these is the remarkable occurrence of a diverse flora including *Psilophyton*, *Protolepidodendron*, and *Archaeosigillaria* reported from Libya by Boureau *et al.* (1978). The plants come from rocks attributed to the top of the Acacus Formation, and accordingly regarded by those authors as of Silurian age. The marine fauna on the age of which the correlation ultimately depends is not actually associated with the plants, but the dating of the flora is established on the basis of the field relationships between the plant-bearing strata and those with marine fauna. The lycopods in this flora include forms attributed to *Archaeosigillaria*; without regard to the generic identity of these plants, lycopods of this general level of leaf cushion development do not appear elsewhere until late Middle or Upper Devonian. Lejal-Nicol (1975) suggests that north Africa may represent the centre of origin of these larger lycopods, invoking slow migration to other regions to explain their delayed appearance elsewhere. Our evidence from other plant groups makes this hypothesis seem improbable. In any event, these



TEXT-FIG. 7. Phylogenetic diagram showing the early Devonian divergence of lycopsids, zosterophylls, trimerophytes, and progymnosperms from rhynialean stock. Sporangia are shown in solid black in the reconstructions, and the positions of protoxylem groups (black) within the steles of the accompanying axial cross-sections.

Libyan lycopods, if of Silurian age, are certainly a puzzling feature in the overall picture of Devonian plant evolution. The possibility that the Acacus fauna is in fact materially older than the plant-bearing section might also be further explored. More evidence is needed to clarify the apparent faunal/floral contradiction here.

An equally puzzling situation has developed with the report by Garratt, quoted in Gray and Boucot (1977), of new graptolite evidence that at least some of the Australian *Baragwanathia* flora is of Ludlow age. In this case, the conflict of evidence concerns the general picture of early land plant divergence. Text-fig. 7 is a diagrammatic presentation of the evidence adduced by Banks (1968), Edwards (1970*b*) and others of the sequential divergence of zosterophylls, lycopods, and trimerophytes from a *Cooksonia*-like Rhynialean stock. Banks has suggested that the exarch zosterophylls with lateral sporangia may have been derived from the centrarch Rhyniales with terminal sporangia; the ensuing derivation of lycopods from zosterophylls, with successive development of an actinostele, enations, and microphyll leaves is consistent with the stratigraphical relationships of these groups (upper part of text-fig. 7). Although the lycopod *Drepanophycus* (not shown in text-fig. 7) occurs more or less contemporaneously with (or possibly a little later than) *Asteroxylon*, the time of first appearance of Rhyniales, Zosterophyllales, and Lycopsida is consistent with the evolutionary relationship suggested here. If *Baragwanathia* is of Ludlow age, this hypothetical phylogeny of vascular plants will require total revision, and our current concept of vascular plant evolution will be seriously challenged. The collective fossil plant evidence seems to favour a Siegenian to Emsian age for *Baragwanathia*. Again, we must await further evidence to clarify this conflict between floral and faunal evidence.

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W. G. CHALONER
ANNE SHEERIN
Department of Botany
Birkbeck College (University of London)
Malet St.
London WC1E 7HX
U.K.